Robson, S., Pinheiro, H., Martins, A., Riul, P., Bruno, S., Janzen, F., & Ioannou, C. C. (2016). The anti-predator role of within-nest emergence synchrony in sea turtle hatchlings. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1834), [20160697]. https://doi.org/10.1098/rspb.2016.0697

The anti-predator role of within-nest emergence synchrony in sea turtle hatchlings

Robson G. Santos[1,*], Hudson Tercio Pinheiro[2], Agnaldo Silva Martins[1], Pablo Riul[3], Soraya Christina Bruno[4], Fredric J. Janzen[5], Christos C. Ioannou[6]

[1] Instituto de Ciências Biológicas e da Saúde, Universidade Federal de Alagoas, Maceió, AL, Brazil

[2] Department of Ecology and Evolutionary Biology, University of California Santa Cruz, Santa Cruz, California, United States of America, and California Academy of Sciences, San Francisco, California, United States of America

[3] Departamento de Engenharia e Meio Ambiente, CCAE, Universidade Federal da Paraíba, Rio Tinto, PB, Brazil

[4] Projeto TAMAR-ICMBio, Escritório Regional de Vitória, Vitória, ES, Brazil

[5] Department of Ecology, Evolution, & Organismal Biology, Iowa State University, Ames, IA, USA

[6] School of Biological Sciences, University of Bristol, Bristol, BS8 1TQ, U.K.

[*]Corresponding author:

E-mail: robsongsantos@gmail.com

Tel/Fax: +55-27-33352527

ABSTRACT

Group formation is a common behavior among prey species. In egg-laying animals, despite the various factors which promote intra-clutch variation that leads to asynchronous hatching and emergence from nests, synchronous hatching and emergence occurs in many taxa. This synchrony may be adaptive by reducing predation risk, but few data are available in any natural system, even for iconic examples of the anti-predator function of group formation. Here, we show for the first time that increased group size (number of hatchlings emerging together from a nest) reduces green turtle (*Chelonia mydas*) hatchling predation. This effect was only observed earlier in the night when predation pressure was greatest, indicated by the greatest predator abundance and a smaller proportion of predators preoccupied with consuming captured prey. Further analysis revealed that the effect of time of day was due to the number of hatchlings already killed in an evening; this, along with the apparent lack of other anti-predatory mechanisms for grouping, suggests synchronous emergence from a nest appears to swamp predators, resulting in an attack abatement effect. Using a system with relatively pristine conditions for turtle hatchlings and their predators provides a more realistic environmental context within which intra-nest synchronous emergence may have evolved.

Keywords: sea turtles, anti-predator behaviour, predation risk, synchronous hatching, attack abatement, dilution effect

INTRODUCTION

Individuals aggregating in temporary or permanent groups is a common behavior among many species. These aggregations may be driven by a variety of reasons, such as defense, foraging and movement efficiency, and considerable attention has been focused on examining the benefits and costs of group formation [1]. Of the proposed explanations for grouping, reducing predation risk is perhaps the most general and is widely believed to be one of the main drivers in the evolution of aggregation behaviour [2–4]. The relationship between prey group size and predation risk has been the target of many studies in a variety of species. Although costs arise from increased conspicuousness ([5–7], although see [8]), aggregation provides benefits because risk is diluted among group members [9], multiple targets visible simultaneously can confuse predators' targeting [10], and predators are more likely to be detected sooner through collective vigilance [11].

The synchrony of sea turtles hatchlings emerging from within a nest is typically believed to reduce predation [12-14], and is often used as a typical example of the anti-predator role of grouping [15] because predation on these otherwise helpless hatchlings is high as they crawl to the sea and swim away from the shore [16,17]. However, studies quantifying hatchling predation are scarce, especially during their crawl from their nests toward the sea [18,19]. Despite the suggestion that synchrony in sea turtle hatching is effective as an anti-predatory strategy, this hypothesis remains to be tested [20]. Peterson et al. [19], using freshwater turtles as a proxy for sea turtle hatchlings, found a decrease in the per capita predation risk with increased group size. Studying predation on a natural system (albeit one under anthropogenic disturbance), Tomillo et al. [18]

found that the number of leatherback hatchlings (*Dermochelys coriacea*) killed by predators had a positive relationship with the number of hatchlings in an emergence. However, they did not present the relationship between per capita risk and group size, leaving it unclear whether dilution counterbalanced the suggested increased encounter rate with predators [20]. Thus, neither of these previous studies demonstrate that synchrony in emerging from a sea turtle nest has an anti-predator role, and it thus remains unknown whether the net effect of aggregation is to decrease per capita predation risk in natural systems [20].

Identifying the mechanism(s) that reduces risk in groups can be a challenging task, especially in observational studies of natural systems due to limitations on monitoring behavioral interactions and control over possible confounding effects [21,22]. For example, while the confusion effect involves predators reducing their rate of attacks or success due to difficultly in targeting [23], and group vigilance relies on coordinated escape responses by prey after predator detection [11], both result in a decrease in per capita risk. As with Foster and Treherne's [9,24] classic water strider (*Halobates robustus*) - fish predator system, however, the potential mechanisms that could reduce risk for synchronously emerging sea turtles are limited. The confusion effect is unlikely to be important as most hatchings and emergences are nocturnal, so that visual cues are limited. Inter-individual signals between hatchlings that could transfer information about the presence of a predator, a requirement for group vigilance, have not been observed, neither have any collective defense strategies. Thus a likely mechanism is attack abatement [4], which relies on an encounter rate with predators that does not increase as fast (or faster) than group size [8], and a dilution effect, which limits the number of prey that are eaten in each encounter [9]. The 'swamping' of predators by synchronous emergence when hatching may occur due to the highly

limited consumption rate by the hatchlings' main terrestrial predator in our study area, the yellow crab (*Johngarthia lagostoma*), as the size of these predators (adults' carapace lengths: 60-120 mm [25]) is relatively close to the typical size of a green turtle hatchling (carapace length: 50 mm [26]). Thus, handling times are expected to be relatively long when a crab captures a hatchling. It is also unlikely that these predators respond quickly enough to a nest emergence so that their encounter with the group is proportional to group size due to the wide distribution of nests over the beach and the limited range over which prey can be detected. Thus, the conditions necessary for attack abatement may be met when sea turtles emerge synchronously, and would be the first demonstration of attack abatement in a vertebrate prey.

Damage to coastal habitats due to anthropogenic activities is so pervasive that opportunity to study and understand natural ecological and evolutionary interactions in coastal communities is rapidly waning [27,28]. Here we investigated in a natural system how group size (i.e. the number of hatchlings emerging together from a nest) influences predation on green turtle (*Chelonia mydas*) hatchlings. Synchrony can also occur in hatching (before emergence) and between nests laid by different females; our study only concerns synchrony of emergence from a nest ('within' nest synchrony). We conducted our study on an oceanic island (Trindade Island, Brazil) that offers relatively pristine conditions for green turtle hatchlings and the yellow crab. The low level of anthropogenic disturbance in this beach environment provides a system that should be relatively representative of the conditions under which intra-nest synchronous emergence evolved.

METHODS

114 *Study Area*

115 Trindade is a volcanic island uplifted 3-3.5 million years ago [29,30], with a
116 total area of 9.2 km² and a narrow platform (0-50 m depth) [31]. It is located ~1,200 km
117 east of mainland Brazil (20°30' S; 29°20' W) with a Brazilian Navy settlement since
118 1957. Trindade is considered the only Brazilian nesting site that has not suffered
119 hunting of female *Chelonia mydas* in recent times. The island is the main nesting
120 ground for green sea turtles in Brazil, hosting ~3,600 nests/year on just 3 km of sand
121 beaches, and is among the most important known rookeries in the Atlantic system for
122 green turtles [32,33]. Thus our study area is a sample of a large population, rather than
123 being a marginal site that may not be representative of nesting grounds for this species.
124 The green sea turtle is the only chelonian that nests on the island and the peak season is
125 January-March [34]. Since 1982, TAMAR-ICMBio has regularly monitored *C. mydas*
126 nests in Trindade. Our study was conducted on Tartarugas beach (300 m in length), the
127 main nesting beach on the island.

128 *Nests and hatchlings group size*

129 We monitored 33 green sea turtle nests that were laid in February and March
130 2009. We placed a circular plastic-mesh corral (50 cm diameter, 50 cm height, 1 cm
131 mesh size) around each nest 40 days after egg deposition to prevent emergent hatchlings
132 from dispersing. This timing was calculated based on incubation durations of nests
133 recorded in previous seasons (43-77 days; TAMAR/ICMBio database). We did not
134 disturb the nests once they were encircled with mesh, allowing hatchlings to emerge
135 without assistance.

136 We visually checked nests every half hour throughout the study from 17:30 to
137 06:00 every night. The corrals remained open 06:00 to 17:00 to avoid hatchling

desiccation in case of diurnal emergence. We checked nests four times daily (10:00, 12:00, 14:00 and 16:00) to count tracks of emerged hatchlings, but these groups were not included in the analysis. We checked the integrity of the corrals constantly during the study period to ensure that no hatchling escaped.

We recorded the following variables to assess group sizes and timing for each emergence from a nest: the order of the emergence event within a nest, the number of hatchlings in each emergence event (group size), and the time of emergence events (hours). We identified an emergence event if at least one hatchling emerged. When we identified an emergence event we waited 10 minutes from the emergence of the last hatchling to ensure that the emergence event was concluded.

Predation

The extant terrestrial fauna of Trindade Island is formed by an unknown number of insect and arachnid species, seabirds, the yellow crab (*J. lagostoma*), the introduced tropical house gecko (*Hemidactylus mabouia*) and mice (*Mus musculus*) [34]. Among all the extant terrestrial fauna, yellow crabs are the most abundant nocturnal terrestrial animal capable of predating green turtle hatchlings. Therefore, we evaluated predation on land focusing on the most abundant predator, yellow crab [34-35]. The yellow crab's absence of a behavioral response to human presence in Trindade Island is long recognized [35]; this naiveté is probably due to the virtual lack of predators when individuals reach the adult phase. This behavior of yellow crabs in Trindade Island helps to minimize any effect of the observers on predator behaviour in our study. Most of the yellow crabs do not live in the beach; they live in burrows in upper vegetated areas and crawl to the beach at night to search for food. Typically they will feed each night, given the opportunity, thus we believe all crabs observed in the surveys were

either actively searching for, or consuming, food. During all the field activities we did not find these crabs engaging in any other behaviors during the night (e.g. reproduction). To quantify crab abundance, we used three parallel 50 m transects, 100 m apart, starting at the high tide line and running inland. We conducted surveys during three time periods (17:30-21:00, 21:00-01:00 and 01:00-05:00) for seven nights during the emergence period of most of the nests (late April to early May). We counted all crabs detected within 3 m of a transect and the number of crabs that had captured a sea turtle hatchling. We considered a crab to have captured prey when we found it holding a hatchling. Due to the large size of the prey relative to the predators, handling times of the prey are long and it is difficult for the crabs to move prey from where they are caught, so are consumed close to the point of capture.

After swiftly counting the hatchlings from an emergence event at a nest site, we turned off our flashlights and released the turtles, allowing them to continue freely crawling toward the sea. We waited a set time until the neonates reached the sea before we turned on the flashlights and searched for depredated hatchlings. We calculated the waiting time based on the distance from the nest to the tide line and a hatchling crawling speed of 5 m/min (sensu Dial [36]). The search for depredated hatchlings was conducted by two observers within 5 m of a transect from the nest to the tide line. To ensure that we counted hatchlings only from a focal nest, we searched the transect area for non-target *C. mydas* prior to releasing the hatchlings.

Statistical Analyses

The total number of crabs in each survey was analyzed as a function of time period (the middle time was used for each period, i.e. 19:15, 23:00 and 03:00) using a Generalized Linear Model (GLM) with a negative binomial error distribution. The

proportion of crabs that captured a turtle hatchling was also analyzed as a function of time period with the polynomial effect of time included after visually inspecting the data (Fig. 1). A GLM with a quasibinomial error distribution was used due to overdispersion.

The number of hatchlings in an emergence event (i.e. group size) was analyzed as a function of the time of day, date, the distance from the nest to the high tide line and the order of emergence within that nest. The analyses were thus carried out at the level of the emergence, i.e. group (n = 51), rather than at the level of the nest (n = 33). Two-way interactions between emergence order and each of the other variables were included. A Generalized Linear Mixed Model (GLMM) with a negative binomial error distribution was used. To test for significant effects, each term was removed in turn from the model and compared to the model including this term. We removed the least significant two way interactions in each model (on the condition that $P > 0.1$) before repeating the process with the remaining terms. All main effects remained in the final model as control variables.

Predation risk was quantified as the number of hatchlings killed as a proportion of the number of hatchlings in each emergence event from a nest. We used a GLMM with a binomial error distribution (glmmPQL was used as the data were overdispersed) to test the effects of group size, time of day, date and the distance from the nest to the high tide line, with two way interactions included between group size and each of the other variables (non-significant interactions were removed as above). To further explore predation risk, we calculated the number of depredated hatchlings found in an evening before the emergence of each group and repeated the analysis of predation risk per groups with this information as an additional explanatory variable.

Nest was included as a random variable in the GLMMs, as multiple emergence events were recorded from some nests. In the analyses, time of day was converted from the 24 hour clock to time elapsed since 00:00 the previous night (e.g. 03:00 was coded as 27 hours). The date was converted in a similar manner from the first date of data collection. All analyses were performed in R 2.15.1 [37].

RESULTS

Prey: green sea turtles hatchling emergence

A total of 3,177 green sea turtle hatchlings emerged from the 33 monitored nests during the study. The vast majority of hatchlings emerged at night (Fig. 1). Diurnal emergence did occur for two *C. mydas* nests, and accounted for only 3.7% of total emerged hatchlings. We observed and recorded data from 2,494 hatchlings in 51 groups. It was not possible to evaluate eight groups (683 hatchlings) due to logistical problems such as storms. From the first emergence to the last, 21 days transpired, with 2.2 groups per night on average. Most nests produced all hatchlings within a single group (Fig. 2), and in cases where multiple groups emerged from the same nest, the number of hatchlings decreased significantly in subsequent emergences (negative binomial GLMM: $deviance_{4,5} = 52.80$, $P = 3.69\times10^{-13}$). The number of hatchlings per emergence (group size) also tended to increase as the season progressed ($deviance_{4,5} = 4.92$, $P = 0.026$), with distance to the sea and the time of day having no effect ($P > 0.5$ in both cases). From all groups that emerged on the same night, only in 7 occasions were the groups less than 2 hours apart. Additionally, in these occasions, the smallest distance between nests was 27.8 m (mean = 86.6 m), which makes interactions between

groups unlikely. Group size varied from 1 to 175 individuals, with an average of 48.9 (S.E. ± 7.6) hatchlings per group.

Predator: yellow crab

The mean density of yellow crabs was 3.70 ± 2.04 crabs/100 m² (range = 1.52-6.67 crabs). Based on beach length (300 m) and distance from the farthest nest to the high tide line (50 m), the mean number of crabs was more than 500 per night. Crab numbers were highest early in the evening and declined during the night (Fig. 1; negative binomial GLM: $LRT_{1,15} = 7.56$, $P = 0.0060$), and the proportion of crabs that were found to have captured a hatchling peaked in the middle time period of 21:00-01:00 (Fig. 1; quasibinomial GLM, polynomial effect of time: $F_{2,14} = 5.95$, $P = 0.013$). This suggests a delay for the predators in becoming active and actually finding prey to consume. Therefore, the number of crabs actively searching for food, and hence representing a risk of predation to emerging hatchlings, was much greater at the start of the night (17:30-21:00) compared to any other time.

Predation

From all 2,494 hatchlings, 2.65% were depredated by crabs prior to reaching the sea. In the analysis of predation risk, only the interaction between group size and time of day was significant (GLMM: $F_{1,16} = 7.59$, $P = 0.014$), with date and distance from the sea having non-significant interactions with group size and main effects ($P > 0.2$ in all cases). The significant interaction was due to predation risk being greater for smaller groups, but only earlier in the evening (Fig. 3*a*, *b*).

To explore why the time of day affected predation risk in small groups, we calculated the number of depredated hatchlings found that evening before the

emergence of each group. Although positively related to the time of day as expected, the two variables were not collinear (Spearman's rank: $r_s = 0.43$, $P = 0.0014$). When this variable and its interaction with group size was included in the model explaining predation risk, the previously significant interaction between group size and time became non-significant (GLMM: $F_{1,12} = 0.47$, $P = 0.51$), while the interaction between group size and number of hatchlings already depredated was significant ($F_{1,15} = 6.20$, $P = 0.025$; all other effects $P > 0.1$). Thus, the effect of time of day on the safety provided by groups could, at least partially, be explained by the number of hatchlings already killed and consumed that evening (Fig. 3*c*, *d*).

DISCUSSION

Our study reveals a pattern of highly synchronous nocturnal emergence within nests, with hatchlings in the majority of nests departing in a single emergence event. The nocturnal emergence will prevent death by overheating and desiccation, and decrease predation by visual and diurnal predators, such as seabirds [38, 39]. Emergence synchrony is predicted to be favored by natural selection [40] because mass departure with large groups of hatchlings should saturate the foraging ability of predators, thereby reducing the predation threat to individuals [12]. Predator satiation is used to explain breeding aggregations that are unpredictable to predators in time and/or space, such as the mast seeding of some plants [41], and large aggregations of invertebrates [42, 43] and vertebrates [44, 45]. Although the large groups formed by marine turtle hatchlings during their emergence from nests have long been predicted to be an anti-predator strategy [15], the relationship between their group size and predation risk remained unknown [20]. Our results provide evidence for this hypothesis: risk was reduced in larger groups, at least early in the evening when the main predator (the

283 yellow crab) was most abundant and also unlikely to already be handling and
284 consuming prey.

285 It has been argued that the risk of detection (i.e. predator avoidance) and the risk
286 of being attacked (i.e. the dilution effect) cannot be considered separately, only the
287 combination of the two will determine if group living reduces predation risk (the attack
288 abatement effect) [4]. However, it is often difficult to isolate predator avoidance and
289 dilution effects from other anti-predatory grouping mechanisms. Of the few explicit
290 empirical studies of attack abatement, none have used a vertebrate prey species
291 [6,46,47]. In our system, the highly stereotyped behavior of hatchlings crawling toward
292 the sea shows no indication of information transfer among individuals, which excludes
293 coordinated evasive behavior such as the 'many eyes' effect. The very limited visibility
294 at night and the small visual range of the main predator relative to the spatial extent of
295 the prey group also makes a confusion effect highly unlikely. The decrease in risk with
296 increased group size may be instead best explained by attack abatement, which relies on
297 an encounter rate with predators that does not increase as fast (or faster) than group size
298 [8], and a dilution effect, which limits the number of prey that are killed in each
299 encounter [9]. The unpredictable and ephemeral availability of hatchlings and the
300 limited ability of the crabs to detect hatchlings from far away should result in a sub-
301 linear (or no) increase in predation relative to group size, a pattern that is widespread
302 [8,32,43,48] even in conspicuous prey [5]. Additionally, the size of the predator relative
303 to prey limits the number of prey consumed per predator per night due to long handling
304 times [49]. These effects are supported by our results which show a delay between the
305 peak abundance of hatchlings and the peak in the proportion of crabs found with prey,
306 suggesting crabs took some time to locate and kill prey, and the importance of the
307 number of prey already killed in a night on predation risk, suggesting substantial

handling times once prey had been found (leading to predator swamping). To demonstrate an attack abatement mechanism more directly, behavioural interactions between hatchlings and crabs could be monitored, for example using infrared lighting or GPS units on crabs to investigate how crabs respond to an emergence from a nest and how their forgaing behaviour changes once a hatchling is captured.

Although our study focused on synchrony of emergence within nests, our results also raise interesting questions regarding the role of female nesting synchrony, i.e. synchrony between nests, and more generally, the interactions between multiple groups regarding when to time exposure to predators. Female nesting synchrony should be favoured to maximise the number of prey available and thus swamp predators [14,50], although predation is only one of potential selective agent that may affect the evolution of reproductive strategies [3]. However, few attempts have been made to test the predator swapping hypothesis [50]. The effects of predator satiation may be stronger for hatchlings that emerge from nests deposited during the peak of the nest season, where 75% of the nests were recorded during 56 days (TAMAR/ICMBio dataset; also see [33]). However, emerging later within an evening was associated with a decrease in risk, particularly for hatchlings emerging in smaller group sizes, due to fewer predators and an increase in the proportion of those already preoccupied with prey. This result suggests that delaying emergence, rather than synchrony, would be advantageous at the scale within the evening. Other factors, such as loss of energy due to catabolism of residual yolk [51,52] and risk of desiccation associated with late emergences [53], would need to be considered, as well as local abundance of both prey and predators. A modelling approach would thus be useful to guide further investigations of these systems (e.g. [45]).

Synchronous emergence is commonly reported to be an anti-predatory behavior for many species [3]. Synchronous hatching in turtles is common and likely to be an ancestral trait [15,40,54], despite the different rates of development within single nests [13,55]. Our study reveals a pattern of high intra-nest synchronicity in emergence and its benefit as an anti-predator strategy for sea turtles. At a mechanistic level, synchrony may arise from social facilitation during ascent through the sand column, as hypothesized by Carr and Hirth [56] and Spencer et al. [13]. It is currently unknown whether individuals hatching in response to hatching nest-mates evolved to reduce risk via increased synchronous emergence, or whether it evolved for reasons other than anti-predator defense (i.e. an exaptation; Gould and Vrba [57]). The timing of emergence may be influenced by other factors, such as physiological (e.g. oxygen levels [58]) and thermoregulatory constraints (e.g. thermal cues that signals hatchlings to emerge from the sand [38,39,59]). Intra-nest emergence synchrony is not universal in all sea turtle nesting areas [60]. More studies under different predation scenarios are needed to clarify this question. However, care must be taken in conducting such studies, because humans have altered most marine coastal ecosystems before modern ecological investigations began and thus the present may not always be the key to the past [28].

ETHICS

This study was conducted under the Brazilian System of Authorization and Information on Biodiversity-SISBIO, license number #19950-1.

DATA ACCESSIBILITY

Data presented in this paper is available as an electronic supplementary material accessible through Dryad (http://datadryad.org/review?doi=doi:10.5061/dryad.h4m68).

AUTHOR CONTRIBUTIONS

R.G.S. and H.T.P.: designed the study; R.G.S. and H.T.P.: collected the data with help from S.C.B.; R.G.S. and C.C.I.: wrote the paper and performed the analysis with help from P.R.; H.T.P., P.R., A.S.M. and F.J.J.: evaluated data and helped draft the manuscript. All authors gave final approval for publication.

ACKNOWLEDGEMENTS

We thank the TAMAR/ICMBio and Brazilian Navy for the logistical support. CCI is supported by a NERC Independent Research Fellowship (NE/K009370/1). We thank the editor and two anonymous reviewers for constructive comments on the manuscript.

REFERENCES

1. Krause, J. & Ruxton, G. D. 2002 *Living in groups*. Oxford: Oxford Univ. Press.
2. Hamilton, W. D. 1971 Geometry for the selfish herd. *J. Theor. Biol.* **31**, 295–311. (doi:10.1016/0022-5193(71)90189-5)
3. Ims, R. A. 1990 On the adaptive value of reproductive synchrony as a predator-swamping strategy. *Am. Nat.* **136**, 485–498. (doi:10.1086/285109)
4. Turner, G. F. & Pitcher, T. J. 1986 Attack abatement: a model for group protection by combined avoidance and dilution. *Am. Nat.* **128**, 228–240. (doi:10.1086/284556)
5. Riipi, M., Alatalo, R. V, Lindstro, L. & Mappes, J. 2001 Multiple benefits of gregariousness cover detectability costs in aposematic aggregations. *Nature* **413**, 512–514. (doi:10.1038/35097061)
6. Wrona, F. J. & Dixon, R. W. J. 1991 Group size and predation risk: a field analysis of encounter and dilution effects. *Am. Nat.* **137**, 186–201. (doi:10.1086/674378)
7. Ioannou, C. C., Ruxton, G. D. & Krause, J. 2008 Search rate, attack probability, and the relationship between prey density and prey encounter rate. *Behav. Ecol.* **19**, 842–846. (doi:10.1093/beheco/arn038)
8. Ioannou, C. C., Bartumeus, F., Krause, J. & Ruxton, G. D. 2011 Unified effects of aggregation reveal larger prey groups take longer to find. *Proc. Biol. Sci.* **278**, 2985–90. (doi:10.1098/rspb.2011.0003)
9. Foster, W. A. & Treherne, J. E. 1981 Evidence for the dillution effect in the selfish herd from fish predation on a marine insect. *Nature* **293**, 466–467. (doi:10.1038/293466a0)

10. Ioannou, C. C., Morrell, L. J., Ruxton, G. D. & Krause, J. 2009 The effect of prey density on predators: conspicuousness and attack success are sensitive to spatial scale. *Am. Nat.* **173**, 499–506. (doi:10.1086/597219)
11. Godin, J.-G. J., Classon, L. J. & Abrahams, M. V 1988 Group vigilance and shoal size in a small characin fish. *Behaviour* **104**, 29–40. (doi:10.2307/4534656)
12. Dehn, M. M. 1990 Vigilance for predators: detection and dilution effects. *Behav. Ecol. Sociobiol.* **26**, 337–342. (doi:10.1007/BF00171099)
13. Spencer, R. J., Thompson, M. B. & Banks, P. B. 2001 Hatch or wait? a dilemma in reptilian incubation. *Oikos* **93**, 401–406. (doi:10.1034/j.1600-0706.2001.930305.x)
14. Tucker, J. K., Paukstis, G. L. & Janzen, F. J. 2008 Does predator swamping promote synchronous emergence of turtle hatchling among nests? *Behav. Ecol.* **19**, 35–40. (doi:10.1093/beheco/arm097)
15. Spencer, R.-J. & Janzen, F. J. 2011 Hatching behavior in turtles. *Integr. Comp. Biol.* **51**, 100–10. (doi:10.1093/icb/icr045)
16. Stancyk, S. E. 1982 Non-human predators of sea turtles and their control. In *Biology and conservation of sea turtles* (ed K. A. Bjorndal), pp. 139–152. Washington, DC: Smithsonian Institution Press.
17. Frazer, N. B. 1986 Survival from eggs to adulthood in a declining population of loggerheads turtles, *Caretta caretta*. *Herpetologica* **42**, 47–55.
18. Tomillo, P. S., Paladino, F. V, Suss, J. S. & Spotila, J. R. 2010 Predation of leatherback turtle hatchlings during the crawl to the water. *Chelonian Conserv. Biol.* **9**, 18–25. (doi:http://dx.doi.org/10.2744/CCB-0789.1)
19. Peterson, C., Fegley, S., Voss, C., Marschhauser, S. & VanDusen, B. 2013 Conservation implications of density-dependent predation by ghost crabs on hatchling sea turtles running the gauntlet to the sea. *Mar. Biol.* **160**, 629–640. (doi:10.1007/s00227-012-2118-z)
20. Heithaus, M. R. 2013 Predators, prey, and the ecological roles of sea turtles. In *The biology of sea turtles, volume III* (eds J. Wyneken K. J. Lohmann & J. A. Musick), pp. 249–284. Boca Raton, FL: CRC Press.(doi:doi:10.1201/b13895-11)
21. Beauchamp, G. & Ruxton, G. 2008 Disentangling risk dilution and collective detection in the antipredator vigilance of semipalmated sandpipers in flocks. *Anim. Behav.* **75**, 1837–1842. (doi:10.1016/j.anbehav.2007.12.016)
22. Cresswell, W. 1994 Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. *Anim. Behav.* **47**, 433–442. (doi:10.1006/anbe.1994.1057)
23. Ioannou, C. C., Tosh, C. R., Neville, L. & Krause, J. 2008 The confusion effect—from neural networks to reduced predation risk. *Behav. Ecol.* **19**, 126–130. (doi:10.1093/beheco/arm109)
24. Treherne, J. E. & Foster, W. A. 1982 Group size and anti-predator strategies in a marine insect. *Anim. Behav.* **30**, 536–542. (doi:10.1016/S0003-3472(82)80066-3)
25. Hartnoll, R. G., Mackintosh, T. & Pelembe, T. J. 2006 *Johngarthia lagostoma* (H. Milne Edwards, 1837) on Ascension Island: a very isolated land crab population. Crustaceana **79**, 197–215. (doi: 10.1163/156854006776952900)
26. National Marine Fisheries Service & U.S. Fish and Wildlife Service. 1991 Recovery plan for U.S. population of atlantic green turtle. National Marine Fisheries Service, Washington D.C.

27. Dayton, P. K. 1998 Reversal of the burden of proof in fisheries management. *Science* **279**, 821–822. (doi:10.1126/science.279.5352.821)
28. Jackson, J. B. C. 2001 What was natural in the coastal oceans? *Proc. Natl. Acad. Sci. U. S. A.* **98**, 5411–5418. (doi:10.1073/pnas.091092898)
29. Almeida, F. F. M. 1961 Geologia e Petrologia da Ilha da Trindade. *Monografia* **18**, 1–197.
30. Greenwood, J. C. 1998 Barian-titanian micas from Ilha da Trindade, South Atlantic. *Mineral. Mag.* **62**, 687–695.
31. Gasparini, J. L. & Floeter, S. R. 2001 The shore fishes of Trindade Island, western South Atlantic. *J. Narural Hist.* **35**, 1639–1656. (doi:10.1080/00222930131709237 9)
32. Seminoff, J. A. (Southwest Fisheries Science Center, U.S.) 2004 *Chelonia mydas*. The IUCN Red List of Threatened Species. Version 2014.3. Available at www.iucnredlist.org
33. Almeida, A. P., Moreira, L. M. P., Bruno, S. C., Thomq, J. C. A., Martins, A. S., Bolten, A. B. & Bjorndal, K. A. 2011 Green turtle nesting on Trindade Island, Brazil: abundance, trends, and biometrics. *Endanger. Species Res.* **14**, 193–201. (doi:10.3354/esr00357)
34. Alves, R .J. V., da Silva, N. G. & Aguirre-Muñoz, A. 2011 Return of endemic plant populations on Trindade Island, Brazil, with comments on the fauna. In *Island invasives: eradication and management* (eds C. R. Veitch, M. N. Clout, & D. R. Towns), pp. 259–263. IUCN, Gland, Switzerland.
35. Lobo, B. 1919 Conferência sobre a Ilha da Trindade. *Arq. do Mus. Nac. Rio Janeiro* **22**, 107–170.
36. Dial, B. E. 1983 Energetics and performance during nest emergence and the hacthling frenzy in loggerhead sea turtles (*Caretta caretta*). *Herpetologica* **43**, 307–315. (doi:10.2307/3892496)
37. R Development Core Team 2011 R: A language and environment for statistical computing.
38. Mrosovsky, N. 1968 Nocturnal emergence of hatchling sea turtles: control by thermal inhibition of activity. Nature **220**, 1338–1339. (doi:10.1038/2201338a0)
39. Drake, D. L. & Spotila, J. R. 2001 Thermal tolerances and the timing of sea turtle hatchling emergence. J. Therm. Biol. **27**, 71–81. (doi:10.1016/S0306-4565(01)00017-1)
40. Glen, F., Broderick, A. C., Godley, B. J. & Hays, G. C. 2005 Patterns in the emergence of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtle hatchlings from their nests. *Mar. Biol.* **146**, 1039–1049. (doi:10.1007/s00227-004-1492-6)
41. Kelly, D. 1994 The evolutionary ecology of mast seeding. *Trends Ecol. Evol.* **9**, 465–470. (doi:10.1016/0169-5347(94)90310-7)
42. Sweeney, B. W. & Vannote, R. L. 1982 Population synchrony in mayflies: a predator satiation hypothesis. *Evolution* **36**, 810–821. (doi:10.2307/2407894)
43. Williams, K. S., Smith, K. G. & Stephen, F. M. 1993 Emergence of 13-Yr periodical cicadas (Cicadidae: Magicicada): phenology, mortality, and predators satiation. *Ecology* **74**, 1143–1152. (doi:10.2307/1940484)
44. Eckrich, C. E. & Owens, D. W. 1995 Solitary versus arribada nesting in the olive ridley sea turtles (*Lepidochelys olivacea*): a test of the predator-satiation hypothesis. *Herpetologica* **51**, 349–354. (doi:10.2307/3893041)

45. Milner-Gulland, E. J. 2001 A dynamic game model for the decision to join an aggregation. *Ecol. Modell.* **145**, 85–99. (doi:10.1016/S0304-3800(01)00381-7)
46. Jensen, K. & Larsson, P. 2002 Predator evasion in *Daphnia*: the adaptive value of aggregation associated with attack abatement. *Oecologia* **132**, 461–467. (doi:10.1007/s00442-002-0979-4)
47. Uetz, G. W. & Hieber, C. S. 1994 Group size and predation risk in colonial web-building spiders: analysis of attack abatement mechanisms. *Behav. Ecol.* **5**, 326–333. (doi:10.1093/beheco/5.3.326)
48. Johannesen, A., Dunn, A. M. & Morrell, L. J. 2014 Prey aggregation is an effective olfactory predator avoidance strategy. *PeerJ* **2:e408**. (doi:10.7287/peerj.preprints.305v1)
49. Holling, C. S. 1959 Some characteristics of simple types of predation and parasitism. *Can. Entomol.* **91**, 385–398. (doi:10.4039/Ent91385-7)
50. Rolf Anker, I. 1990 The ecology and evolution of reproductive synchrony. Trends Ecol. & Evol. **5**, 135–140.(doi: 10.1016/0169-5347(90)90218-3)
51. Hays, G. C., Speackman, J. R., Hayes, J. P., Speakman, J. R. & Hayes, J. P. 1992 The pattern of emergence by loggerhead turtle (*Caretta caretta*) hatchlings on Cephalonia, Greece. *Herpetologica* **48**, 396–401.
52. Godfrey, M. H. & Mrosovsky, N. 1997 Estimating the time between hatching of sea turtles and their emergence from nest. *Chelonian Conserv. Biol.* **2**, 581–585.
53. Matsuzawa, Y., Sato, K., Sakamoto, W. & Bjorndal, K. A. 2002 Seasonal fluctuations in sand temperature: effects on the incubation period and mortality of loggerhead sea turtle (*Caretta caretta*) pre-emergent hatchlings in Minabe, Japan. *Mar. Biol.* **140**, 639–646. (doi:10.1007/s00227-001-0724-2)
54. Colbert, P. L., Spencer, R. J. & Janzen, F. J. 2010 Mechanism and cost of synchronous hatching. *Funct. Ecol.* **24**, 112–121. (doi:10.1111/j.1365-2435.2009.01602.x)
55. Gyuris, E. 1993 Factors that control the emergence of green turtle hatchlings from the nest. *Wildl. Res.* **20**, 345–353. (doi:10.1071/WR9930345)
56. Carr, A. & Hirth, H. 1961 Social facilitation in green turtle siblings. *Anim. Behav.* **9**, 68–70. (doi:10.1016/0003-3472(61)90051-3)
57. Gould, S. J. & Vrba, E. S. 1982 Exaptation; a missing term in the science of form. *Paleobiology* **8**, 4–15.
58. Ackerman, R. A. 1980 Physiological and ecological aspects of gas exchange by sea turtle eggs. Am. Zool. **20**, 575–583.
59. Glen, F., Broderick, A. C., Godley, B. J. & Hays, G. C. 2006 Thermal control of hatchling emergence patterns in marine turtles. J. Exp. Mar. Bio. Ecol. **334**, 31–42. (doi:10.1016/j.jembe.2006.01.005)
60. Houghton, J. D. R. & Hays, G. C. 2001 Asynchronous emergence by loggerhead turtle (*Caretta caretta*) hatchlings. *Naturwissenschaften* **88**, 133–136. (doi:10.1007/s001140100212)

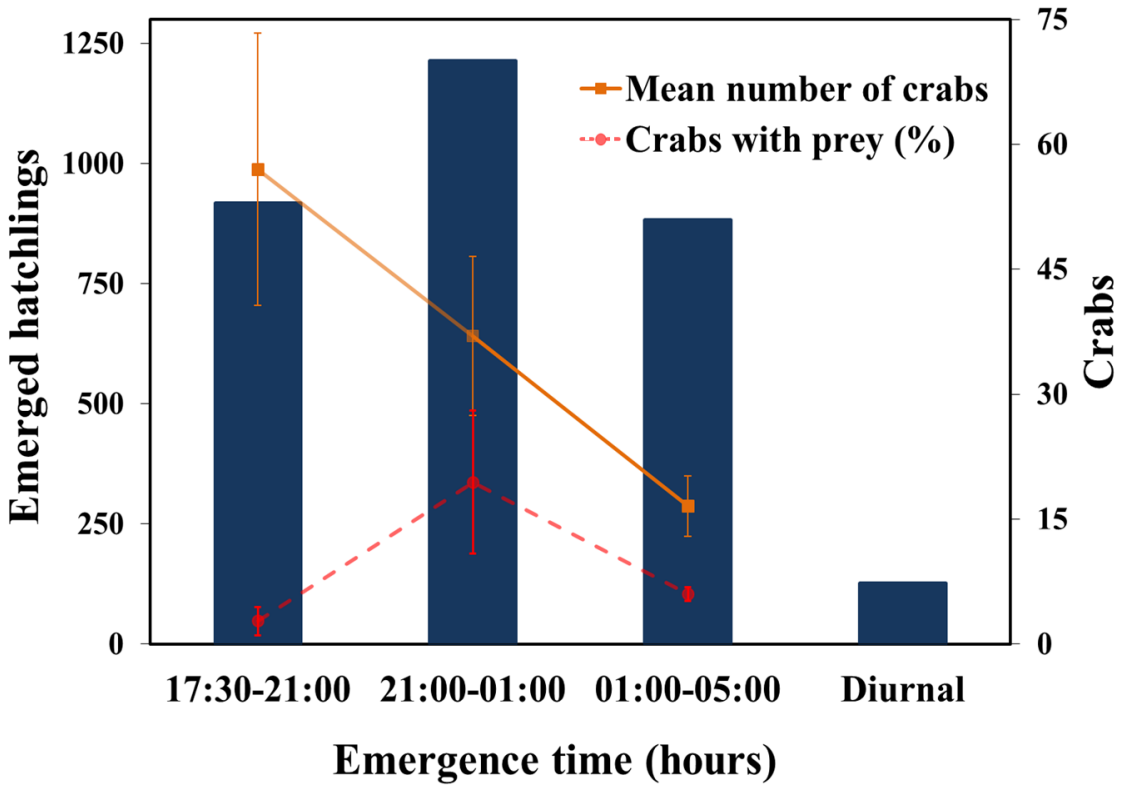
FIGURE LEGENDS

Figure 1 – Temporal distribution of emerged green turtle hatchlings (columns, data from the nest emergences); mean (± SE) density of yellow crabs at night (orange line), and mean (± SE) relative number of crabs that have captured a green turtle hatchling (red dashed line, data from crab surveys).

Figure 2 – Number of emergence events per nest for the 33 green turtle nests from Trindade Island, Brazil.

Figure 3 – Determinants of predation risk in green turtle hatchlings. Per capita predation risk is represented by bubble area; groups without any mortality (i.e. zero risk) are represented by diamonds. Risk is plotted against group size and time of day (a, b) or number of prey already killed that evening (c, d). (a) and (c) show the observed risk per group, while (c) and (d) show the fitted (i.e. predicted) risk from Generalised Linear Mixed Models with the two axes as interacting covariates and nest as a random factor.

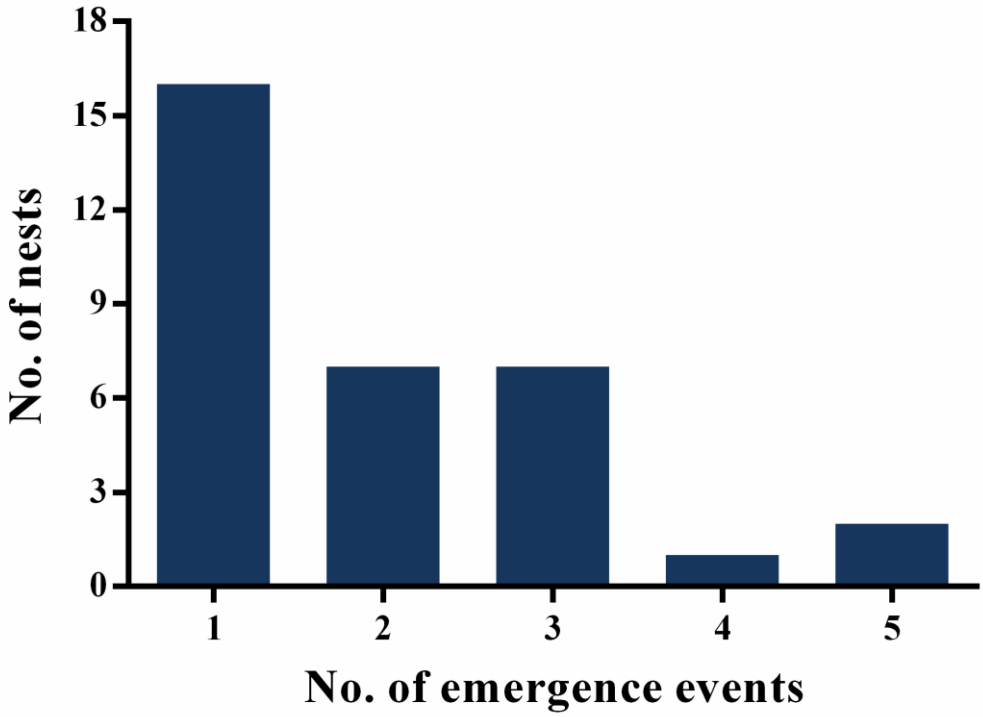
548 Figure 1



549

550

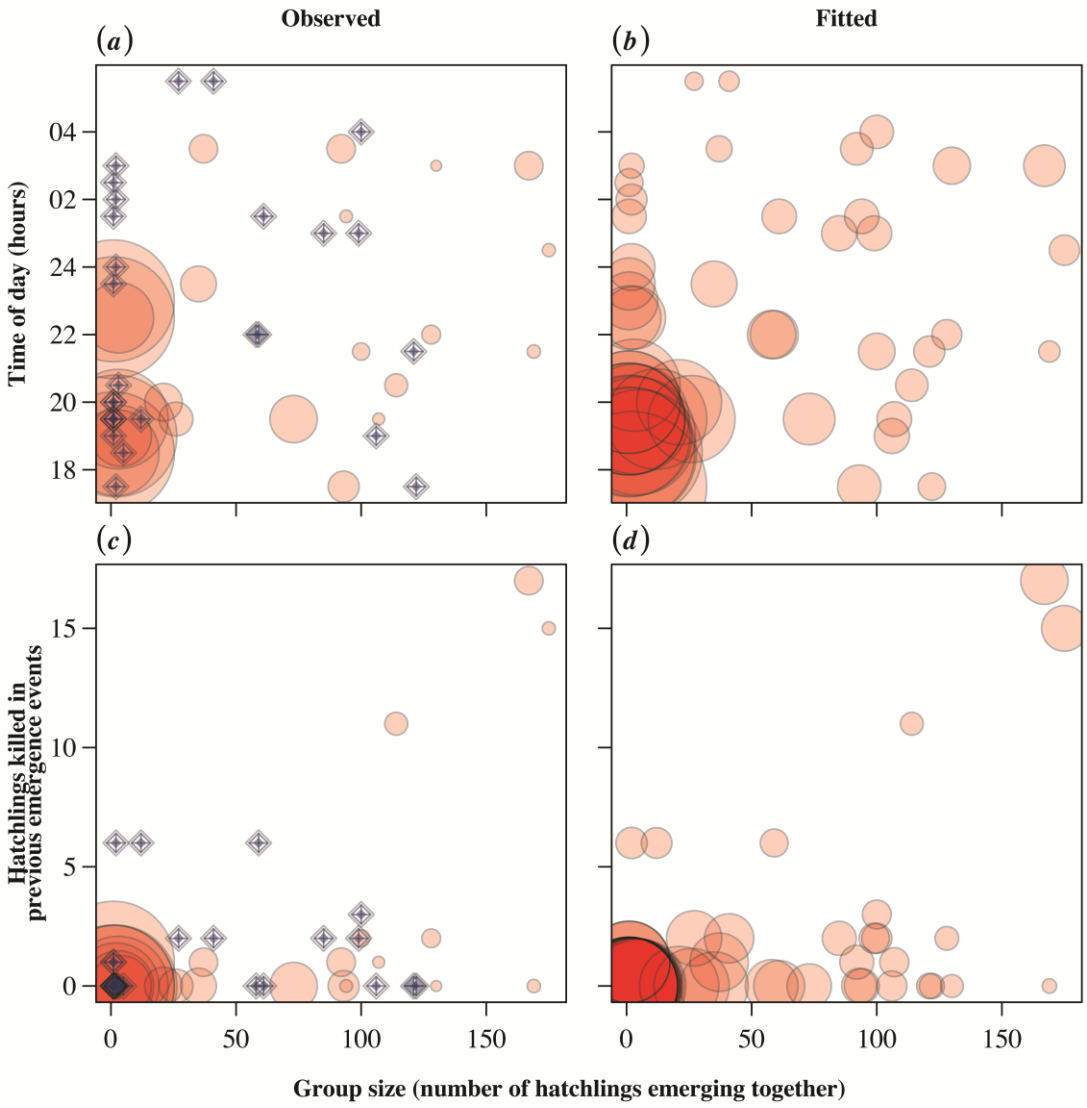
551 Figure 2



552

553

554 Figure 3



555